five in number. Of these, 61% have a single secondary line, 30% two secondary lines, 8% three secondary lines and 1% have five secondary lines. When more than one line are present they are usually initiated at the same stage in the growth of the individual.

Dr. Schenck[3] suggested that these secondary lines are related to the age of the specimen. To check on this the occurrence of secondary lines was charted against age of the individuals. As lines of growth are not consistent, this was measured in terms of length in millimeters along the main line of primary bifurcation.

Secondary lines were found beginning at from 2 to 12 mm. along the main primary line. The majority, however, start at about 8 mm. This is construed to mean that secondary lines tend to be initiated when the individual is about half grown.

The results of this study may be briefly summarized as follows: (1) The main line of primary bifurcation crosses the shell at an angle which gives evidence of being distinctive for the species. (2) Various primary patterns are present, reasons for which are not established, and which do not seem important as specific characters. (3) Secondary lines of bifurcation are present in about two-thirds of the specimens examined and when present are definitely related to age of the individual.

A STUDY OF THE VARIATIONS IN THE RADULA OF A SNAIL WITH PARTICULAR REFERENCE TO THE SIZE OF THE MEDIAN TEETH*

BY SAM W. HOWE

I. Introduction

In 1856, C. Troschel began his systematic study of the radulae of molluscs. Since then malacologists have lacked agreement in the interpretations which have been placed

[3] Personal communication.

*Contributions from the Zoological Laboratory of the University of Illinois, No. 360.

upon radular characters in the classifications of gastropods. While some workers have maintained that the radula provides safe criteria for generic and specific diagnosis, others have ignored radular characters or have denied their validity. E. W. Bowell (1924) implies that radular characters must be used with discretion in specific diagnosis. H. M. Gwatkin (1914) says that the redular characters do not always have the same value in the diagnosis of genera or species, "Often it is decisive, sometimes useless" is the way he states it. A. E. Boycott (1914) concludes that for the radula to yield characters of any value in classification, the size of the animal must be stated with the description of the radula. Friele (1879) regards the radula as possessing characters of little value in classification of species as compared with external characters. E. W. Bowell (1920) maintains "that certain characters (of the radula) formerly relied upon for determination of species are unimportant."

Despite these conflicting views held by outstanding investigators, very little has been done to establish specifically the constancy or variability in radulae of individual species. Some observations have been published on the changes within the radula during individual development from embryo to adult. V. Sterki (1893), in working on the radulae of embryos and adults of some ten species of snails, discovered distinct changes in the shape of the teeth, number of rows of teeth, and number of teeth in the rows, from embryo to adult. The number of rows and the number of teeth in each row were found to increase with advance in age of the animal. He even expressed the view that one may think of it as a "true metamorphosis" of the radula.

Most of the workers who have given attention to this problem have confined themselves to the number of rows, number of teeth in each row, and the size of the whole radula. F. G. Cawston (1926), while examining the radulae of snails that were intermediate hosts of parasitic trematodes in Natal, observed that the number of rows and number of teeth in each row differed in small and large individuals. A. E. Boycott and J. W. Jackson (1914), in working on *Helicella heripensis* and *H. caperata*, found the number of rows and the number of teeth in each row to increase definitely with increase in size of shell. A. E. Boycott (1914) determined that the size of the whole radula, and the number of transverse rows in the radula increased definitely with the increase in size of the shell of Hyalina. A. H. Cooke (1918) found the number of denticles to be variable in a number of gastropods. E. W. Bowell (1908) also found the number of teeth in the Helicids to vary and concluded that "the number of teeth in any given radula may be a matter of comparatively little importance". M. V. Lebour (1906) noticed variation in the number and shape of teeth in the radulae of certain Buccinidae but she saw "no correlation of variation with regard to the radula and the shell".

For the most part, however, recent malacologists have assumed that specific variations in the radula are non-existant, or at least unimportant. Particularly has this been true in the assumptions regarding the size of the individual teeth. Some have gone so far as to say that there is no variation in the size of the individual teeth (Sterki, 1893). However, Boycott (1914) after finding the number of rows in the radula of Hyalina to vary from 38 to 48 and the estimated number of teeth to vary from 850 to 1,632, concluded that the "increase in size (radula) which accompanies growth is mostly due to an increase in the size of the individual teeth". He estimated the size of the teeth, however, rather than measured them.

Dr. H. J. Van Cleave of the University of Illinois suggested that the writer undertake a detailed study of the radulae in certain fresh-water gastropods to determine the reliability of radular characters in taxonomic studies. This problem has consequently been pursued under his direction. The writer also wishes to express his indebtedness to Mr.

Frank C. Baker who gave much valued assistance during the progress of the study.

Materials and Methods: As the initial object of this investigation, snails of the genus *Goniobasis* were selected because of the relatively simple radula formula characteristic of the family Pleuroceridae. The specimens which have served as the basis for this investigation were collected from the Salt Fork at Homer Park, Illinois, in June and July, 1929. Through the courtesy of Mr. Calvin Goodrich, the specimens upon which this investigation has been carried out were identified as *Goniobasis livescens* Menke.

The radula of *G. livescens* has only seven longitudinal rows of teeth. The formula for *G. livescens* as given by Baker (1928) for individuals from Wisconsin is

$$\frac{1}{8\text{–}9}\quad\frac{1}{5\text{–}6}\quad\frac{1}{5}\quad\frac{1}{4\text{–}1\text{–}4}\quad\frac{1}{5}\quad\frac{1}{5\text{–}6}\quad\frac{1}{8\text{–}9}$$

The radula formula of specimens used in this study was found to vary from that published by Baker. I found the formula in the specimens under observation to be

$$\frac{1}{9\text{–}12}\quad\frac{1}{5\text{–}7}\quad\frac{1}{5}\quad\frac{1}{3\text{–}1\text{–}3}\quad\frac{1}{5}\quad\frac{1}{5\text{–}7}\quad\frac{1}{9\text{–}12}$$

There seemed to be some variation in this formula as in one or two specimens the median tooth was like that found by Baker,

$$\frac{1}{4\text{–}1\text{–}4}$$

Concerning the differences in the formulas recorded by Baker for *G. livescens* and by the present writer, no final conclusion may be drawn at this time. However, it should be kept in mind that the specimens were from two distinctly different localities. Individuals figured by Baker were from relatively large rivers in Wisconsin, while the objects of the present investigation were from a small stream in Illinois. Superficially the shells of specimens from the two localities seem to be identical, and have been so determined by Goodrich, but the radular differences here set forth may serve as a basis for distinguishing ecologically distinct variations of *Goniobasis livescens.*

The radulae under investigation were extracted with NaOH 40%, stained with chromic acid 1%, dehydrated in 95% alcohol, and mounted in diaphane.

Three measurements of the shells are given for comparing the size of individuals. This was done because in some cases the apical whorls of the shells were decollated. This would make some slight difference in the relative sizes. In no case, however, was there much decollation of the apical whorls. This fact invalidated the use of the number of whorls as a practical criterion for determining age.

Statement of Problem: An analysis of the reliability of radular characters in the taxonomy of gastropods involves so many problems that only a few have been selected for this initial study. The most significant aspects of the problems treated in this paper are:

1. An accurate determination of variability in size of median teeth in the same radula, whether graded variation from one end to the other, chaotic, or definitely correlated with worn, functional, and newly developing regions of the radula.
2. An examination of the influence of age upon the relative width of the median teeth, as encountered in snails of different sizes.
3. Relative widths and length of the central cusp on the median teeth of radulae from snails of different sizes with especial reference to change in size of central cusp with change in size of median teeth.

II. Observations on Radulae

Morphology: Three regions are readily distinguishable in the radula though they are not sharply delimited, for one grades without distinct boundary into another. The oldest, anterior-most portion bears about 15 to 35 transverse rows of somewhat broken and very much worn teeth. Adjacent to this worn region is a portion in which the teeth are all perfect and not noticeably worn. The posterior region of the radula bears teeth in the process of development. These new teeth comprise 14 to 20 transverse rows which by the technique here employed take very little or no stain.

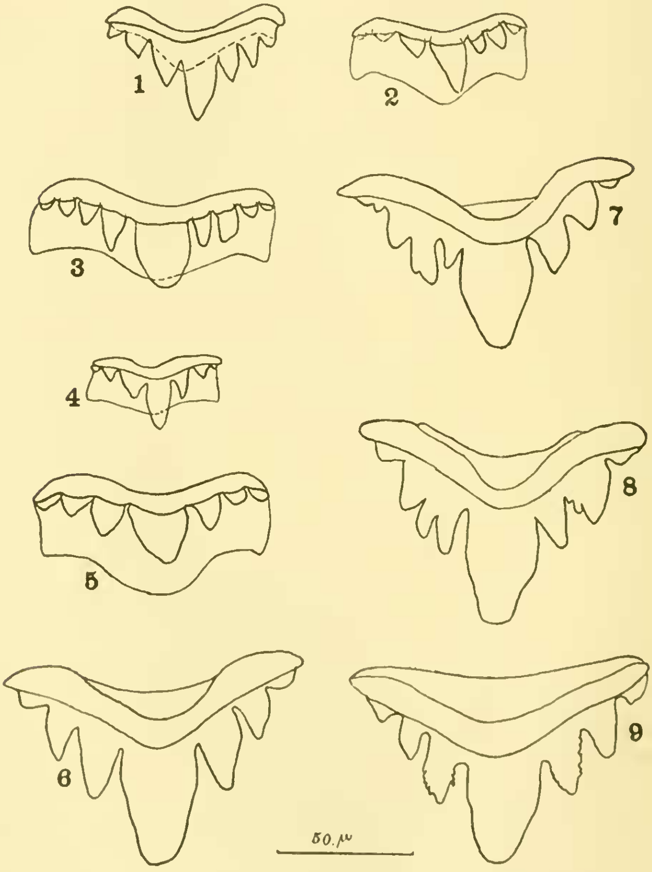
Variability of median tooth. A. *In the same radula.* Six entire radulae were examined to determine the variation in size of the median teeth in the same radula and the relation of this variation to the position of the teeth in the radula. The widths of the median teeth were found to vary as much as 14μ (78μ to 92μ), in the same radula. In four of the radulae, the teeth in the undeveloped region were the smallest (70μ to 78μ), the teeth in the oldest or worn region were largest (76μ to 96μ), and the teeth in the perfect region were between these two in size (74μ to 88μ). Thus we have evidence of a definite increase in size from the younger region to the older region of the same radula. In the other two radulae, the teeth in the perfect region were the largest (44μ to 54μ) while there was very little difference in the size of the teeth from the other two regions. In one case the teeth in the older region (40μ to 44μ) were a little larger than in the undeveloped region (40μ) and in the other case the teeth in the undeveloped region were so arranged on the slide that measurements in that region were impossible. These conditions, found in the two last mentioned radulae, have not been explained.

B. *In different radulae.* The other radulae examined showed variations in widths of median teeth in the same radula as great as 16μ (from 84μ to 100μ, in specimen 29, Table I). By pressure on the cover glass, the radulae were broken so that isolated teeth were available for accurate measurement and drawing but due to this isolation the original position of the teeth in the radula could not be determined. From the results obtained in the examination of the six entire radulae, it seems probable that the size differences in the same radula depend very largely upon the position of the teeth in the radula and are not chaotic. These results are shown in Table 2.

Variability in the central cusp. A. *Width.* The measurements of five entire radulae yielded the results shown in Table. 3. This table shows in three of the five radulae, a definite progressive increase in width of the central cusp of the median teeth from the undeveloped end to the worn or oldest part of the radula. In specimen number 47 (a small shell 5.8 mm. in length) the central cusp on the older end were narrower (8μ) than those in the perfect region (10μ). In specimen number 42, the central cusps in the perfect region (21μ) and the worn region (20μ) were practically the same in size. The results shown in Table 1 are the measurements of central cusps in isolated median teeth in the radulae of some 40 broken up radulae. The differences in width of central cusps in the radulae of the same individual were as great as 8μ (16μ to 24μ) in specimen 27. The size differences shown here are probably correlated with position in the radula as in the five entire radulae mentioned above. This could not be determined because of the shifting of the teeth from the original position during the process of isolating them. It is probable, however, that the width of the central cusp varies directly with position in the radula as does the width of the entire median tooth.

B. *Length.* The lengths of the central cusps of the median teeth are also shown in Table 1. In the five entire radulae, the central cusps of the perfect teeth are the longest. The central cusps of the worn teeth are about the same length (16μ in specimen 37) as those of the undeveloped region (16μ in specimen 37) though in some cases the worn cusps are shorter (6μ to 15μ in specimen 46). This decrease in length of the central cusp of the worn teeth is due to the wear to which they have been subjected. The lengths of the central cusps were found to vary from 2μ to 14μ in the individuals that were broken up in isolating the median teeth.

Correlation of Tooth and Shell Size. Forty two specimens



Figs. 1 to 5. Central teeth from radulae of *Goniobasis livescens* showing range in size and variability in number and arrangement of the cusps.

Figs. 6 to 9. Central teeth from the radula of the same individual showing a normal tooth (6) and different types of abnormality (7 to 9) occurring in the same radula.

of Goniobasis varying in length of shell from 5.6 mm. to

20.8 mm. were examined for variations in size of median teeth of radulae from different animals. Even a superficial glance at the data shown in Table 2 gives conclusive evidence that tooth size varies directly with body size. Variations in width of median tooth from 40μ in the smallest specimens to 108μ in the largest specimen were found. Some digressions from a progressive increase in width of median tooth with increase in length of shell were discovered. These can be explained in the variations within the individual radula mentioned above. There is a definitely uniform increase in the size of individual teeth of radulae from different individuals progressing with increase in size of shell. This does not show so well from looking at the smallest or largest tooth of a given radula and comparing it with that next in size. However, it is shown in the overlapping of the sizes of the teeth in different radulae. In the radula from all shells 10.9 mm. to 20.8 mm. in length some individual teeth may be found that are approximately 80μ in width. If the width of every tooth in every radula were compared with the width of the corresponding tooth in every other radula, the correlation of increase in size of teeth and shell would probably be still closer.

The differences in width of individual teeth from different radulae seem to be as great in the larger snails as in the smaller individuals, showing a range from 44μ to 68μ in shells from 7.5 mm. to 8.4 mm. in length and a range from 78μ to 108μ in shells from 10.6 mm. to 20.8 mm. in length.

Variability in Number of Teeth. There were considerable variations in the number of transverse rows of teeth in the six entire radulae examined. These variations were from 68 transverse rows in specimen 46, from a shell 12.3 mm. in length, to 112 transverse rows in specimen 41 whose shell was 20.0 mm. in length. The increase in number of rows coincided progressively with increase in size of shell. No instances of variations in the number of teeth in each transverse row were observed, each row consisted of seven teeth which is the constant, normal number for the species.

In most of the recorded variations in the radulae of other genera of snails, by Sterki (1893), E. W. Bowell (1908), A. E. Boycott (1925), F. F. Cawston (1926), A. E. Boycott (1914), and M. V. Lebour (1906), there were definite variations found in the number of teeth in the transverse rows. Most of the radulae studied by the above named investigators were those having a relatively large number of comparatively small teeth in each transverse row, while *G. livescens,* used in this study, has a relatively small number of comparatively large teeth in each transverse row.

The results obtained in the present investigation show no variations in number of teeth in each transverse row but a definite variation in size of individual teeth, while the above investigations show definite variations in number of teeth in each transverse row but no conclusive evidence of variation in size of individual teeth. This may mean that in radulae of few but large teeth, the variation is in size of individual teeth, while in radulae of many but small teeth, the chief variation is in number of teeth.

Continuity of Abnormality in Teeth. H. M. Gwatkin (1914) maintains that any abnormality found in the teeth in a radula will be continued posteriorly through the longitudinal row in which it occurs. In one specimen (No. 12) used in this investigation, some of the central teeth were abnormal. However, the abnormality was not uniform throughout the entire row. There were a number of malformed teeth in the central row (figures 7, 8, 9) each one of which had a distinctive type of malformation. Some of the teeth in the same longitudinal row were perfectly normal (figure 6). The relative positions of the malformed teeth in the row could not be determined because the teeth were isolated. That they were all from the same row is self-evident because each radula has but a single row of central teeth.

III. Summary and Conclusions

1. The number of transverse rows in the radulae *G. livescens* increases definitely with increase in the size of the shell but there is no variation in the number of teeth in each transverse row.

2. A distinct increase in the size of the individual median teeth and the central cusp of median tooth in radulae of *G. livescens* accompanies increase in size of the shell. The increase is fairly uniform from very small animals to comparatively large individuals.

3. Distinct differences in size, both of the central cusp and of the entire median teeth, occur in individual radulae of *G. livescens*. There is progressive increase in size of the tooth and its central cusp from the undeveloped end to the worn end of the radula.

4. Malformations in the radula may be chaotic i.e. not continuing uniformly throughout the longitudinal row.

5. In using radular characters in classification, the size of the shell must be recorded with the description of the radula. The width of median teeth has no value in specific diagnosis of Goniobasis unless snails of practically the same size are used in every case. The size of the median teeth in young snails can not be used in specific diagnosis in comparison with radulae from older snails, for tooth size increases directly with age. Thus in species showing wide divergence in size of the mature shells, a comparison of radulae from shells of the same size could not yield a valid basis for comparison of the two species.

Table 1. Relation between size of shell, central cusp, and entire median tooth in 42 individuals of *Goniobasis livescens*.

Spec. No.	Length of shell in mm.	Greatest diameter of shell in mm.	Length of Aperture in mm.	Central Cusp of Median tooth Length in μ	Width in μ	Width of Median tooth in μ
15	5.6	2.7	3.0	10–12	8	44–50
47	5.8	3.1	2.9	13–16	6–10	40–50
48	5.9	3.1	2.9	14–16	9–10	48–54
23	6.0	3.3	3.2	18	7–8	44–48
24	6.5	3.5	3.7	14	8	48–54
45	7.1	3.6	3.9	16–18	9–10	56–60
20	7.5	4.0	3.7	12–14	8–11	40–56
31	7.5	4.0	3.8	12–20	8–16	44–56
33	7.5	3.6	3.7	10–12	8–16	52–56
44	7.5	3.8	4.0	20–24	12–16	52–60
17	8.0	3.9	4.0	.....	.....	62–64
36	8.2	4.3	4.5	16–20	10–12	60–68
18	8.4	4.0	4.3	20–24	12–16	56–62
32	10.9	5.7	5.7	20–24	12–14	68–72
35	12.0	5.7	5.7	16–24	16	84
2	12.1	6.0	5.9	.....	.....	86–88
46	12.3	5.8	6.2	18–28	14–18	76–84
25	12.4	6.1	6.1	22–24	16–18	68–80
43	12.5	6.1	6.4	14–21	16	70–76
34	12.6	6.4	6.4	20–22	16	74–76
26	12.7	6.0	6.1	20–24	18–20	64–76
27	13.3	7.3	7.8	18–32	16–24	88–92
16	13.6	6.4	6.6	28	20	84–88
22	15.8	7.8	8.5	20–26	14–18	80–84
28	15.8	7.2	7.3	20	16	80–82
42	16.1	7.4	7.5	24–32	16–21	80–92
19	16.4	7.3	7.4	30	22	80–84
3	16.7	7.9	7.7	.....	.....	74
30	17.4	7.9	7.7	20–26	16–20	80–84
7	17.8	7.8	8.1	24–36	20–24	102–108
13	18.4	8.0	8.0	35	28	90–100
21	18.4	7.7	7.6	20	20	92–96
29	18.4	8.1	8.6	30–36	22	84–100
37	19.0	8.3	8.3	21–22	16–20	82–88
10	19.5	7.9	8.0	44	24	100
40	19.6	8.4	8.7	16	18–20	84–96
6	19.8	7.9	7.7	.....	.....	96–102
39	19.9	8.6	8.6	32–36	22–26	88–96
41	20.0	8.6	8.9	20–26	18–22	78–92
38	20.2	8.0	8.1	16	18–20	84–92
12	20.6	8.5	9.0	.....	.....	104–108
14	20.8	8.9	9.10	24–28	24–28	100–104

TABLE 2. Showing (a) correlation of size of shell and number of transverse rows of teeth in radulae of *G. livescens*, and (b) variation in size of median teeth in relation to position on radula.

Spec. No.	Length of shell in mm.	Number of transverse rows in Total	Post. Undev.	Per-fect	Ant. worn	Width of individual teeth in μ Post. Undev.	Per-fect	Ant. worn
47	5.8	88	15	53	20	40	44–50	40–44
46	12.3	68	15	35	18	..	50–54	48
43	12.5	97	14	63	20	70	74	76
42	16.1	104	10	79	15	80	84–88	90–92
40	19.6	107	18	56	33	..	84–88	96
41	20.0	112	15	80	17	78	84–88	90–92

TABLE 3. Showing variation in lengths and widths of central cusp in relation to position in the radula of *Goniobasis livescens.*

No. of Specimens	Region	Length in μ	Width in μ
47	Undeveloped	14	6
	Perfect	16	10
	Broken	12	8
45	Undeveloped	15	8
	Perfect	17	9
	Broken	6	10
43	Undeveloped	12	10
	Perfect	19	15
	Broken	12	17
42	Undeveloped	24	16
	Perfect	29	21
	Broken	16	20
37	Undeveloped	16	14
	Perfect	18–20	16–20
	Broken	16	20

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NEW CALIFORNIAN SNAILS

BY H. A. PILSBRY

A sending last June from Mr. Stanley C. Field of Los Angeles contained an apparently new race of *Helminthoglypta traskii* and a *Haplotrema* closely allied to one which had been recognized as new for some time, but not yet described.

HELMINTHOGLYPTA TRASKII FIELDI n. subsp. Pl. 5, figs. 2, 3, 4.

The shell is more elevated than *H. t. phlyctaena*, the height 74 to 77 percent of the diameter (in *phlyctaena* 60 to 66 percent); umbilicus smaller, about 2 mm. wide; post-nuclear whorls are not papillose; last 2½ whorls are spirally engraved with lines cutting the striae, strongly developed on the last whorl. Color cinnamon-brown, with a darker, chestnut-brown band broadly bordered on both sides with chamois. Peristome